SUN COMPASS ORIENTATION OF PIGEONS UPON EQUATORIAL AND TRANS-EQUATORIAL DISPLACEMENT

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The operation of the sun compass in northern latitudes has been established in numerous arthropods, reptiles, fish and birds (von Frisch, 1950; Pardi and Papi, 1952; Birukow, 1960, Gould, 1957; Fischer, 1961; Hasler *et al.*, 1959; Braemer, 1959; Kramer, 1952a, 1952b; von St. Paul, 1953). The utilization of this mechanism for actual field orientation has been demonstrated in many arthropods (von Frisch, 1950; Pardi and Papi, 1952 and others) and pigeons (Schmidt-Koenig, 1960, 1961); it has been shown likely that it is used by turtles (Gould, 1957) and fish (Hasler *et al.*, 1960).

A large number of field studies of migratory birds has revealed the prevalent role of directional orientation (Rüppel, 1944; Rowan, 1946; Rüppel and Schüz, 1948; Perdeck, 1958; Lack, 1959, 1960). The actual application of the sun compass during migration has not yet been proven. However, if the sun compass were applied, birds whose migrational routes cover many degrees of latitude or lead to equatorial or trans-equatorial regions would encounter rather striking changes in the sun's angular velocity (both azimuthal and directional). Braemer (1960) particularly has pointed to the complex nature of a full scale sun compass which must operate at grossly different latitudes and different seasons. Something comparable to an almanac would be necessary to master all significant variables.

It is evident that an examination of the performance of the sun compass under extreme solar conditions is inevitable. Southward latitudinal displacement has been carried out in the past with bees by Kalmus (1956) and Lindauer (1959) and with fish by Hasler and Schwassmann (1960).

In this, the first of a series of experiments, the present author examined the operation of the sun compass in a stationary training apparatus in homing pigeons raised at Durham, N. C., upon displacement to Belém, Brazil and Montevideo, Uruguay, in fall, 1961. We are aware of the fact that pigeons as non-migratory birds may well differ in their orientational capacities from migratory birds. This species was, nevertheless, chosen as experimental subject because it handles best in experiments and because the translocation expedition was expected to be too difficult to be accomplished on the first try with small migratory passerines. We will call upon those later.

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Duke University). I would like to particularly acknowledge the special efforts undertaken by both agencies to facilitate the expedition to South America. I am much indebted to Dr. H. O. Schwassmann for his stimulating and helpful role. The experiments reported here were initiated by discussions with H. O. Schwassmann at the 25th Cold Spring Harbor Symposium in 1960. H. O. Schwassmann also must be credited for his effort in the founding of a colony of pigeons at Belém, Brazil, of birds from the Wilhelmshaven and the Duke University strain [1] which will be used for further joint experiments there. I am grateful to Dr. Peter H. Klopfer for his steady helpfulness and support; further, to the late Dr. Walter A. Egler, Director of the Museu E. Goeldi, Belém, Brazil, and his successor Dr. Eduardo Galvão, to Dr. Jose Maria Conduru, director of the Instituto Agronomica do Norte, Belém, Brazil, for their extremely helpful cooperation; to Drs. Paul Ledoux and Werner Sattler (then at Belém) for their kind assistance; last, but not least, to Prof. Dr. Victor Bertullo, director of the Departamento de Investigaciones Pesqueras, Universidad de Montevideo, Montevideo, Uruguay, for his most helpful efforts to facilitate the experiments there. I am grateful to Peter H. Klopfer for critically reading the manuscript.

Material and Methods

In order to avoid the bias of the hand-operated device originally inaugurated by Kramer (1952d), and also used by von St. Paul (1953), Hoffmann (1954; 1960), Rawson (1954), and modified by Rawson (unpubl.) and Schmidt-Koenig (1958; 1960), a semi-automatically operating apparatus for the directional training of pigeons was designed (Fig. 1).

Twelve pecking discs, attached to micro switches, are mounted symmetrically at the periphery of a circular cage, one meter in diameter. Landmarks are screened by a removable aluminum wall. A food cup whose cover can be opened and closed either manually or by a solenoid is inserted into the center of the floor. This portion of the apparatus rests on a base of bakelite upon which it can be rotated.

The base contains 12 electrical contacts, each of which is connected to an electromagnetic counter mounted in a separate box. Also mounted in this box is a 6-volt battery, a relay to operate the solenoid and a time delay to keep the food cup open for several seconds at a time. The contact (*i.e.,* the compass direction) which is to activate the solenoid that opens the cover of the food cup for rewarding a correct choice can be selected by a rotary switch. Each pecking disc is wired to a brush which rests on the contacts in the base. Upon proper rotation of the upper portion (by hand) only that particular disc, the direction of which coincides with the desired training direction, can activate the rewarding mechanism. In addition, each disc activates a counter corresponding to the direction to which it points. The entire apparatus is portable so as to facilitate long-distance transport.

After 3–4 days of starvation, the birds, first, were taught to walk to and peck at a disc and to walk back and look for food in the center cup. This took a

[1] Birds from the Wilhelmshaven strain have been imported to and are being bred at Duke University. Differences in the orientational abilities of the two strains are the subject of another paper.

pigeon about two hours to learn. Then the bird had to learn to peck at a disc in one particular compass direction (the training direction). Only correct choices activated the rewarding mechanism. This took a pigeon several weeks to learn. During training the cage was irregularly rotated; during the final stages of training, rotation was according to a random number table (the Rand Corporation, 1955) with a range of 1–10 or 5–15 positions. For the training, the apparatus and the birds were transported to various open places in the immediate vicinity of

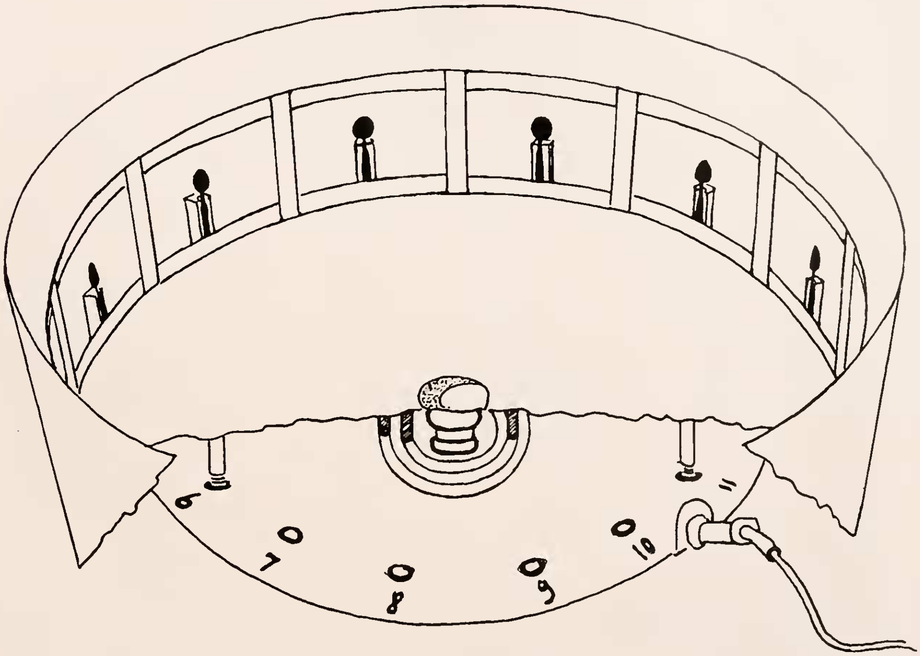

FIGURE 1. Perspective section view of the training apparatus. Six of the twelve black pecking discs are shown above their sockets which house the micro switches. Netting, through which the birds peck at the discs, lines the circular framework around the discs; other netting covers its top. In the center of the upper platform the food cup is indicated. Underneath the upper platform, brushes (hatched) are shown in contact with metal rings centered on the base through which the rewarding is operated. Six of the twelve contacts are depicted in the base (Nos. 6–11) and two of the twelve brushes subtending from the upper platform to contacts Nos. 6 and 11. For more details see text.

Duke University where the apparatus was set up on top of a pickup truck. At other times the birds were housed in an aviary at the Duke Forest lofts.

Five pigeons, offspring of the Wilhelmshaven strain bred at Duke University, were subjected to directional training on May 2, 1961; the training continued through mid-September, 1961, with 3–4 training sessions per week. The training direction was to the south. The training time varied between 8:45 and 14:45 true local time (Fig. 2). In each session, each bird was allowed to work for about 20 minutes. From June 15, 1961, on, each bird had to perform 5 unrewarded choices, from July 1 on, 10 unrewarded choices, and from August 1 on, 20 unrewarded choices before the rewarded training started. The direction of the mean vector of these unrewarded choices from each session after July 24, 1961, when the training seemed to have taken shape, are given in Figure 2.

In the critical tests in South America the birds had to perform 10–20 unrewarded choices in each session. This took, usually, less than 10 minutes. The cage was rotated irregularly between choices. A little while after the choices, the birds were allowed to feed from the hand-operated cup. There was no training in South America.

The mean vector of all choices of each session has been calculated according to Gumbel, Greenwood and Durand (1953). For statistical evaluation, the procedure and tables of Greenwood and Durand (1955) and Durand and Greenwood (1958) and graph derived from these (Schmidt-Koenig, 1961, appendix), respectively, have been used to discriminate between random and non-random samples. Non-random samples ($p \leq 0.05$) were plotted in black symbols (Figs. 2–3); those random above the 5% level in open symbols. If statistics could not be applied, due to small sample size ($n < 6$), an open symbol with a central point is plotted. Unfortunately, no specific method to compute the confidence limits of mean vectors is yet available.

Solar and experimental data have been calculated and plotted with reference to true local time (TLT), allowing for the equation of time. All solar data have been taken from the Nautical Almanac for 1961 and the Tables of Computed Altitude and Azimuth (see references).

Experiments and Results

Durham, N. C.

Figure 2 gives the performance of the birds between July 25, and September 14, 1961, at Durham, 36° 00′ N; 78° 56′ W. Three seasonally characteristic sun azimuth curves are also depicted in Figure 2. All birds compensated rather well for the local sun's movement. The majority of choices falls into the range for spring and summer; however, the scatter is too large to decide whether or not the birds are able to allow for the specific seasonal rate of change of azimuth of the sun.

The translocation experiment was planned for the fall equinox of 1961. This would provide the least change in day/night ratio and would permit tests under the zenith sun. Unfortunately, political events in Brazil delayed the travel until the end of September. The birds were trained the last time at Durham on September 14, 1961. From September 25 on, they were accommodated in a covered transportation crate and prevented from directly seeing the sun except during their individual testing periods.

Belém, Brazil

Birds and apparatus were flown to Belém during the night of September 27, 1961. In Belém, the apparatus was set up on top of a flat-roofed building at the Instituto Agronomico (1° 27′ S; 48° 25′ W) which had no tall landmarks around it. A time shift of about two hours clockwise was involved in the translocation. The adjustment of the birds' internal clock is known to take less than two days under natural conditions.

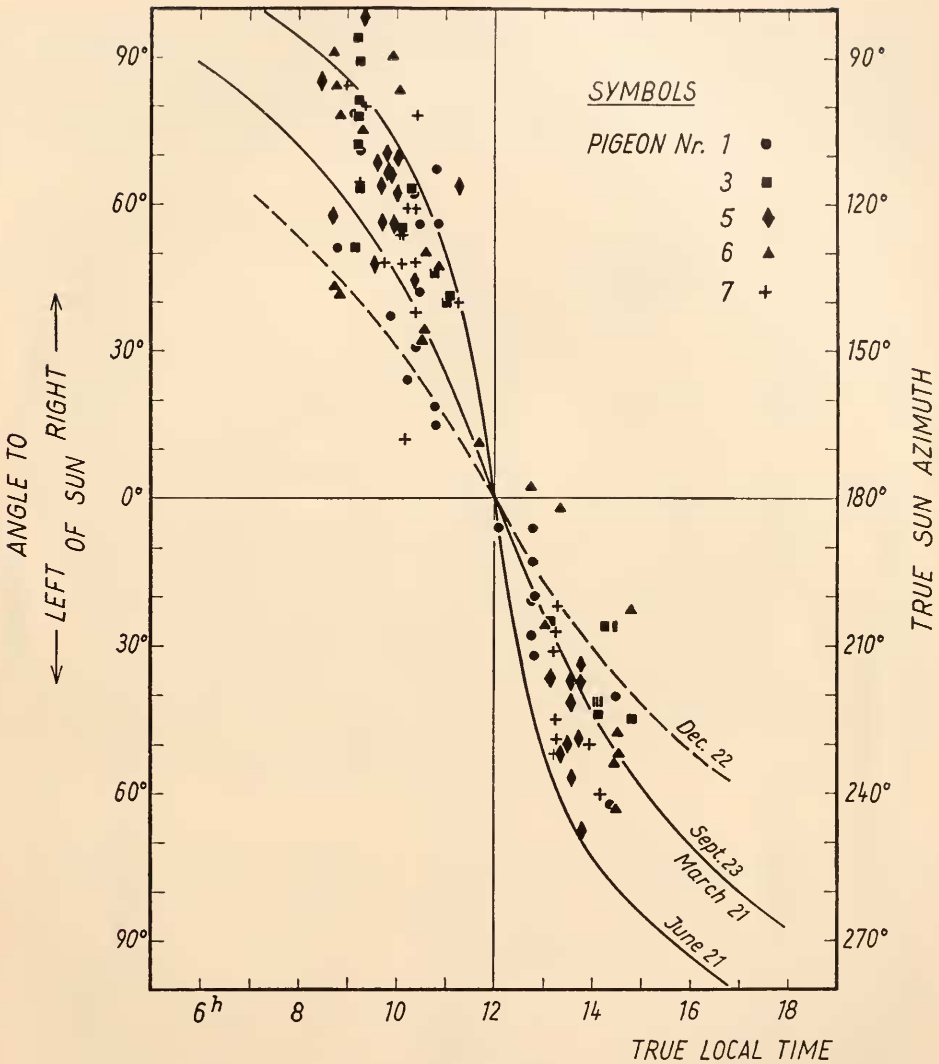

FIGURE 2. The performance of the 5 birds at Durham, N. C., between July 24 and September 14, 1961. Each symbol represents the direction of the mean vector of all unrewarded choices (n = 10–20) during one examination session performed at the time of day indicated on the abscissa and plotted as angle to the actual sun azimuth position (left coordinate). The curves for the summer solstice and for the equinoxes are drawn as solid lines; the birds' training fell in this period of the year.

Birds No. 1, No. 5, and No. 6 were chosen for the equatorial tests. No bird reacted at all in the first testing session on September 29 at 11:50 to 12:22 TLT. From September 30 on, No. 1 and No. 6 cooperated rather well when placed into the apparatus, exceptionally up to three times per day. If the birds were reluctant to peck, this may, at least to some extent and particularly during the first days of examination, have been due to the frequent appearance of vultures in the sky, which obviously frightened and immobilized the birds. No. 5, however, was already very unstable in its readiness to cooperate during its training in Durham. It turned to rather erratic choices in Belém as can be seen from Figure 3. The total number of successful examinations of all birds may be taken from Figure 3.

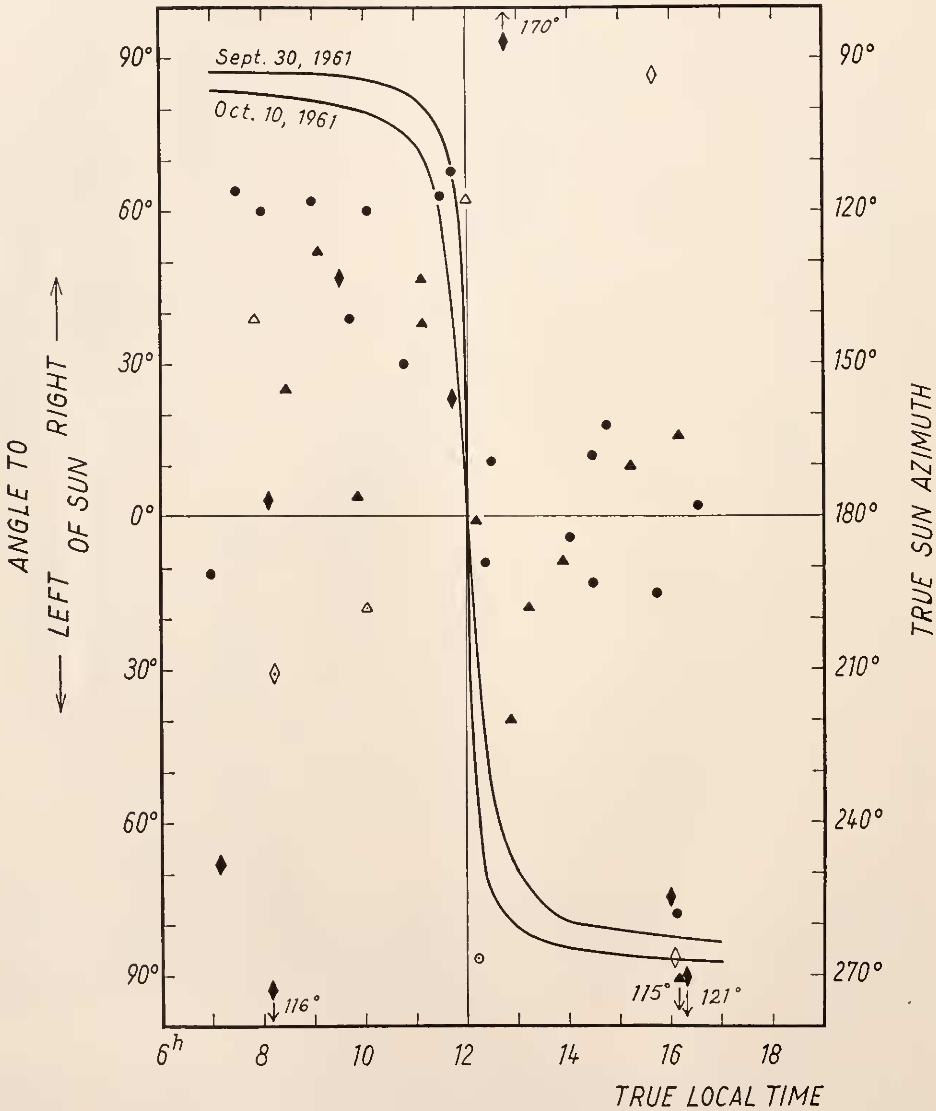

FIGURE 3. The performance of pigeon No. 1, No. 5, and No. 6 at Belém, Brazil, between September 30 and October 10, 1961. The local sun azimuth curves are drawn for these dates. Symbols and way of plotting as in Figure 2. An open symbol was plotted for random choices.

The last examination was performed on October 10, 1961. Figure 3 also gives the local sun azimuth curves for the first and the last day of examinations.

During the forenoon (neglecting pigeon No. 5), the bird's reference to the azimuth position of the sun conforms with that at Durham rather than with the actual local condition; however, the scatter is very large. The majority of choices performed during the afternoon was well off the usual range. The direction actually indicated by the birds shifted to the west. Hasler and Schwassmann (1960) seem to have encountered a similar phenomenon, although the choices of their fish tended to be at random rather than pointing in particular, however "wrong," directions. It should be indicated at this point that in the Montevideo tests, all birds compensated for the sun's movement much more in accordance with their performance at Durham, also during the afternoon. Pigeon No. 5 worked even more reluctantly than at home. In addition, its few choices were rather erratic. Its scores, therefore, are neglected in view of the more decisive performance of the other birds.

The day of zenith culmination was missed, as pointed out earlier. However, 7 tests of pigeon No. 1 and No. 6 were held when sun altitudes were more than 80°. The respective scores of these tests, which fell within local noon time ± 35 minutes, can easily be located in Figure 3. Only in one instance (pigeon No. 6 at 12:08 at a mean sun altitude of 87°) were the choices ($n = 9$) at random with $p > 0.1$. The other scores that are at random (pigeon No. 1 at 12:16) are due to small sample size ($n = 2$). In the remaining 5 tests at sun altitudes of 81°–84° only two (pigeon No. 6 at 12:18 and pigeon No. 1 at 12:27, both at sun altitudes of 82°) conform with the expectation. Thus, since the whole pattern of scores is rather widely scattered, the precise range of sun altitudes at which the birds are unable to derive compass directions from the sun has yet to be established.

Montevideo, Uruguay

Birds and apparatus were flown from Belém to Montevideo on October 12, and 13, 1961. Tests were performed from October 16 through November 2, 1961, in an open field east of Montevideo at 34° 53′ S; 56° 05′ W. The time shift involved in the translocation was less than one hour counterclockwise. There was ample time for the birds to become synchronized with the local day. Pigeons No. 3 and No. 7 were principally called upon; however, despite their extensive tests at Belém, No. 1 and No. 6 turned out to be still cooperative, as may be seen from Figure 4. Towards the end of the Montevideo time, however, the readiness of all birds to choose was nearly exhausted. The total number of successful tests may be taken from Figure 4. Also plotted in Figure 4 is the mirror image of the sun azimuth curve for Montevideo of October 24, 1961, the medium date of examinations and the azimuth curve for Durham for the same date. The true azimuth curve for Montevideo would fall outside the main figure and is, therefore, plotted in the inserted figure on a full 360° scale.

Again, the birds clearly did not allow for the actual sun movement. The pattern of scores conforms more nearly to that at Durham (Fig. 2); however, the variance appears to be considerably larger. Also, there seems to be a trend to the west around noon and during the afternoon but far less than in the Belém tests. This westward shift may have been caused by the fact that the training at Durham never

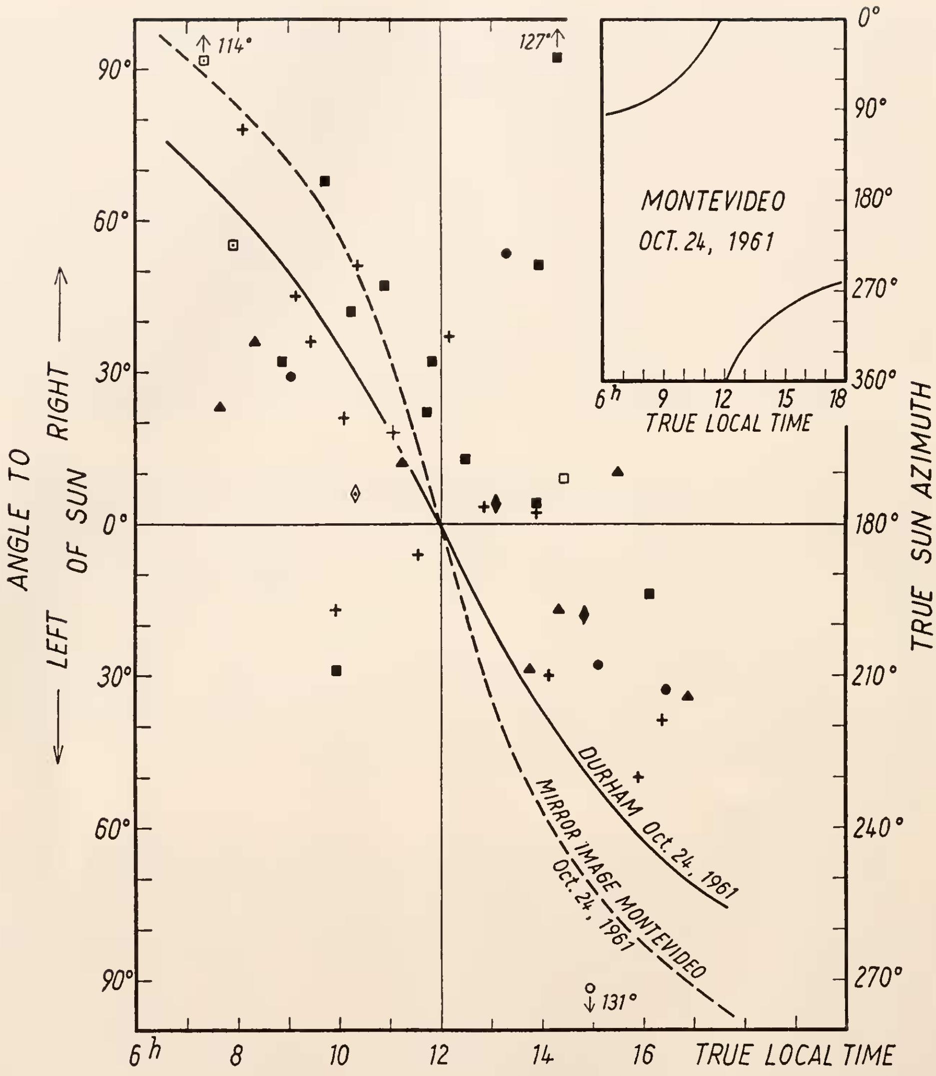

FIGURE 4. The performance of the 5 birds at Montevideo, Uruguay, between October 16 and November 2, 1961. Also plotted in the main portion is the sun azimuth curve for Durham for October 24, 1961 (solid line), as the medium date of examinations and the mirror image of the corresponding curve for Montevideo (broken line). The actual sun curve for Montevideo is depicted on a 360° scale in the inserted figure. Symbols and way of plotting as in Figures 2 and 3.

extended beyond 15:00, while testing at Belém and Montevideo extended until 17:00, involving westerly sun positions. A tendency to follow the sun rather than to maintain a fixed direction and increase the angle to the sun is frequently observed under conditions unfamiliar to the animal.

Discussion and Conclusion

From the scores of the pigeons it can be safely concluded that they did not allow for the equatorial or trans-equatorial sun movement. The birds seem to have largely referred to the sun as if it were the sun at Durham. The scores in South America, though mostly significantly non-random, appear to be more widely spread than those at the training place. It remains unanswered whether this may be interpreted as a specific reaction resulting from the disagreement between orientational features expected by the bird and those actually observed, or as a nonspecific result of handling the bird in unusual and strange conditions, however irrelevant to orientation, or simply as a fading of the training. Nevertheless, the short period of exposure to the local sun of about 10 minutes was clearly insufficient to allow the bird to take full acount of the discrepancies between local solar parameters and those at home. Nonetheless, migratory birds or the navigating pigeons should be able to take account of these within that time period if the sun is the basis for navigation. Previous experiments on the sun compass in northern latitudes failed to demonstrate solar altitude as a source of information for directional choices in starlings and pigeons (Hoffmann, 1954; Schmidt-Koenig, 1958). A number of specifically designed homing experiments did not support solar altitude as providing navigational information to pigeons (Kramer, 1953, 1955, 1957; Rawson and Rawson, 1955; Hoffmann, 1958; Schmidt-Koenig, 1958, 1961).

The homing pigeon, a nonmigratory species, was chosen for this initial series, because of its technical advantages. That it is not an entirely irrelevant subject for studies of sun compass orientation in equatorial regions may best be illustrated by a non-specific account: it is illegal to keep homing pigeons in Brazil because they are extensively used for smuggling diamonds and narcotics. This speaks for their reliability in homing, at the very least.

A new series of experiments is under way in which pigeons, raised and trained at Durham, N. C., will be exposed to the local conditions in South America in an aviary several months in advance of tests. This procedure may reveal whether individuals are able to adjust to grossly different solar conditions. The present series may serve as a control experiment.

In the translocation experiments with bees (Kalmus, 1956; Lindauer, 1959, see also 1960) the examinations concerned offspring of displaced individuals rather than the translocated individuals themselves. Kalmus (1956) claims that even the offspring did not adjust to the new solar conditions. Lindauer (1959) clearly demonstrated in his experiments that the offspring allowed for the equatorial sun movement. This apparent controversy has not been settled yet. Another relevant experiment was concerned with displaced fish (Hasler and Schwassmann, 1960). The authors consider their data as preliminary and exploratory and only drew tentative conclusions. It is unfortunate that the majority of the scores of their fish so far published are in fact not very convincing, due to a sample size just too small for statistical evaluation and to too large variance. This is, in turn, due to specific difficulties arising from work with fish.

Summary

1. Five homing pigeons were directionally trained at Durham, N. C. (36° 00′ N; 78° 56′ W). An automatically recording and rewarding cage was used. The

directional response of the birds was tested upon displacement to Belém, Brazil (1° 27′ S; 48° 25′ W) and subsequently to Montevideo, Uruguay (34° 53′ S; 56° 05′ W). The birds were prevented from directly seeing the sun except for the actual test periods of about 10 minutes on each occasion.

2. The birds clearly did not allow for the respective local sun movements in South America but referred to the sun as if it were the sun at Durham. The choices in South America were more widely scattered than those at home.

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